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SEQUENCE ANALYSIS OF COURTSHIP BEHAVIOR IN THE DIMORPHIC JUMPING SPIDER *MAEVIA INCLEMENS* (ARANEAE, SALTICIDAE)

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ABSTRACT. Males of the dimorphic jumping spider, *Maevia inclemens* differ in both morphology and courtship behavior. Transition matrix analysis was conducted to determine what differences in male behavior and female receptivity were statistically significant. While males are both morphologically and behaviorally distinct, there was a high degree of overlap in the courtship sequences. The primary difference between males was the standing posture used by the tufted morph to attract female attention from a distance and the prone posture used by the gray male at close proximity to the female. When these behaviors were included in the analysis as separate behaviors, there was a significant difference between transition matrices for the male morphs. However, when these behaviors were combined and called "Phase I courtship" there were no significant differences between the morphs nor in the female responses to male behavior.

The dimorphic jumping spider, *Maevia inclemens* Walckenaer (also known under the name *vittata*), is a jumping spider commonly found in the eastern and midwestern USA. In *M. inclemens*, the two male morphs differ dramatically in both morphology and behavior (Peckham & Peckham 1889, 1890; Emerton 1961; Painter 1913, 1914; Barnes 1955; Jackson 1982). Barnes (1955) and Kaston (1972) described the males as variable in coloration: in one variety (tufted) the body is black with three tufts of setae on the anterior cephalothorax, the legs are pale and unmarked (except for black band near the tips of legs I) and the palps are generally jet black (Fig. 1a); in the other morph (gray) the body has black to brown chevrons over a pale ground color, and the sides of the abdomen and legs have many oblique bars. Additionally, the gray morph is never found with tufts, instead having a pale horizontal color bar on the anterior cephalothorax above the median and lateral eyes and yellow to orange pedipalps (Fig. 1b). Lacking tufts and orange palps, females are characterized by a rust colored dorsal abdomen and a conspicuous white stripe below the anterior eyes.

Previous observations by Peckham & Peckham (1889) and Painter (1913, 1914) showed that male dimorphism in *Maevia inclemens* involved not only morphological differences but differences in courtship behavior. However, the descriptions of courtship behavior by Peckham & Peckham (1889) and Painter (1913) do not fully agree. The Peckhams claimed that the gray male, upon approaching a female, raised its first pair of legs (either so as to point them forward or upward), keeps the palpi stiffly outstretched, and bends the tip of the abdomen down toward the substratum. They observed this behavior when males were at distances of 6–8 cm from the female. This was followed by a dance display where legs I were clapped together while the male zig-zagged from side-to-side (Fig. 2b). Next, the Peckhams claimed that as the gray male approached the female its body was lowered to the substratum, at the same time legs I were dropped and it assumed a prone or crouched position (where legs I and II were pointed forward so that the tips touch in front and the proximal joints were held almost perpendicular to the body at right angles). After assuming this prone position, the gray morph moved in a semicircle before the female, sometimes advancing, sometimes receding (Fig. 1b). Painter (1913) disagreed with this description of the gray morph courtship behavior. He did not observe the raised leg with stiff palp display and reported that the prone position was assumed first by the gray male when it recognized the female. After this, the male raised the front legs and performed the leg clapping zigzag dance described above.

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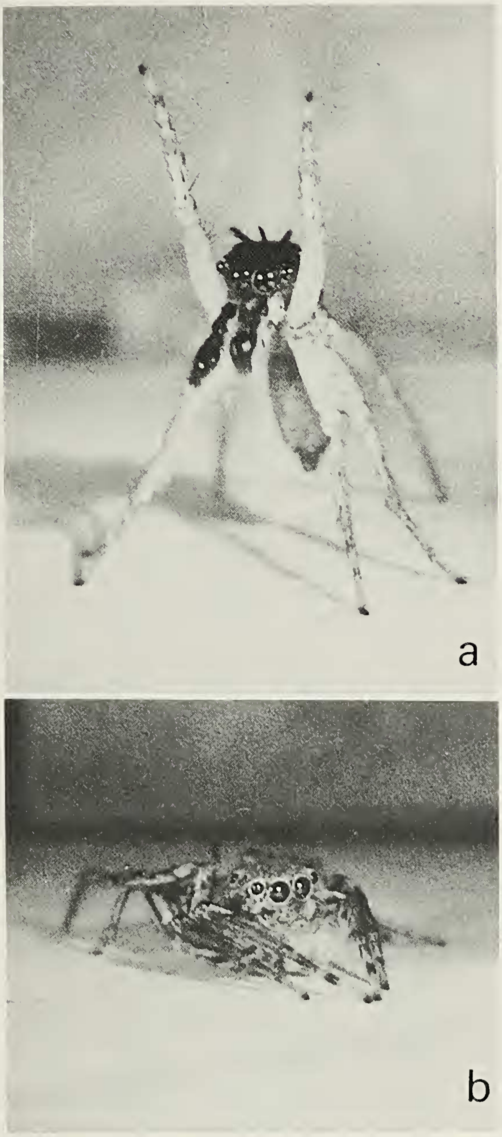

Figure 1.—Initial reaction of male *Maevia inclemens* upon sighting a female. a. Tufted morph. After sighting a female, the tufted morph stands up (STILTS) and waves legs I vigorously in an opening and closing pattern, while at the same time waving the pedipalps up and down, and swinging the abdomen from side to side; b. Gray morph. In contrast, the gray morph crouches down (PRONE) and points legs I and II directly forward (crossing the tips of the legs and creating a triangle-like configuration) while holding the orange colored pedipalps beneath the anterior eyes, and gliding back and forth in stationary or receding semi-circles in front of the female.

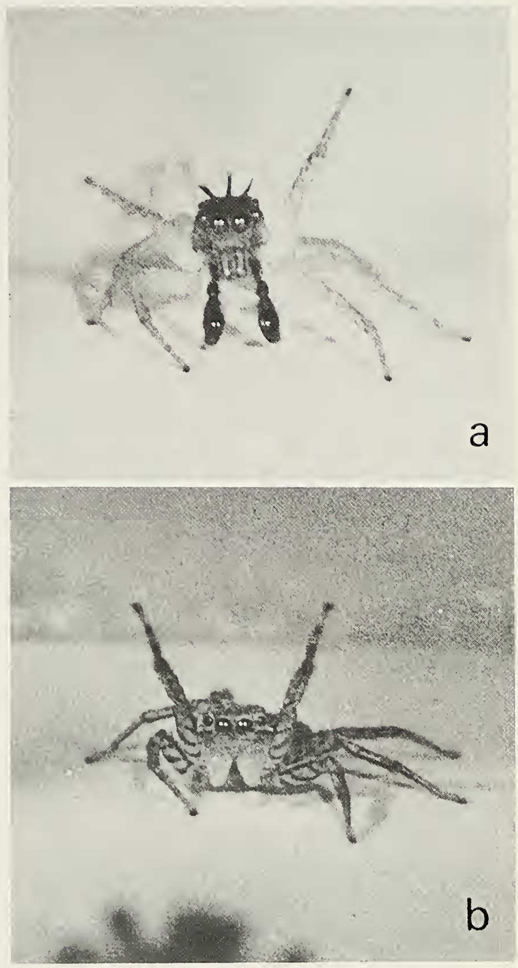

Figure 2.—Second phase reaction of male *Maevia inclemens* upon sighting a female. a. Tufted morph performing the LEG CLAPPING display during the second phase of courtship where males approach the females to mate; b. Gray morph performing the LEG CLAPPING display.

Descriptions by the Peckhams (1889) and Painter (1913) on the courtship display of the tufted morph are in agreement. After sighting a female the tufted morph stood up or stilted, the first pair of legs was held above the cephalothorax and waved to and fro, cyclically (Fig. 1a). Neither Peckham & Peckham (1889) nor Painter (1913) reported on the tufted male performing the leg clapping zig-zag dance display after the stilt display. However, as will be reported here, this display is typical of tufted males (Fig. 2a) and demonstrates that while males are behaviorally distinct during one phase of the courtship sequence, the motor patterns of the two morphs

Table 1.—Tufted morph transition matrix (n = 30 Tufted males). Column of letters (far left) represents the corresponding behavior (e.g., A = MLMVE; BB = FEORNT, etc.). Top number in a row is the observed value and the bottom number is the expected value. Row Chi Square values are given in the far right column.

	Following acts								
	Tufted male								
Preceding acts	B. MLOR-NT	C. MLAPP	D. STILT	E. PRONE	F. LGCLP	G. MLLG-FRN	H. CHASE	I. MLJMP	J. MNTC-OP
Tufted male									
A. MLMVE	0	0	0	0	0	0	0	0	0
exp.	0.32	0.15	0.27	0.00	0.96	0.36	0.30	0.12	1.40
B. MLORNT	0	6	5	0	5	0	0	1	0
exp.	1.25	0.56	1.06	0.00	3.70	1.49	1.15	0.48	5.43
C. MLAPP	0	0	3	0	1	0	0	0	0
exp.	0.48	0.22	0.41	0.00	1.43	0.58	0.45	0.19	2.10
D. STILT	0	0	0	0	0	0	0	0	0
exp.	0.89	0.41	0.75	0.00	2.63	1.06	0.82	0.34	3.85
E. PRONE	0	0	0	0	0	0	0	0	0
exp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F. LGCLP	0	0	0	0	0	4	0	4	0
exp.	3.14	1.45	2.66	0.00	9.31	3.75	2.90	1.21	13.67
G. MLLGFRN	0	0	0	0	0	0	0	0	19
exp.	1.29	0.60	1.09	0.00	3.82	1.54	1.19	0.50	5.61
H. CHASE	0	0	0	0	11	0	0	1	0
exp.	0.85	0.39	0.72	0.00	2.51	1.01	0.78	0.33	3.68
I. MLJMP	0	0	0	0	2	0	0	0	5
exp.	0.40	0.19	0.34	0.00	1.19	0.48	0.37	0.16	1.75
J. MNTCOP	0	0	0	0	0	0	0	0	49
exp.	4.43	2.05	3.75	0.00	13.13	5.29	4.09	1.71	19.27
K. DISMNT	1	0	0	0	13	1	0	0	14
exp.	2.66	1.23	2.25	0.00	7.86	3.17	2.46	1.02	11.56
L. MLRUNA	0	0	0	0	0	0	0	0	0
exp.	0.64	0.30	0.55	0.00	1.91	0.77	0.60	0.25	2.80
Female									
AA. FEMVE	17	0	0	0	0	0	0	0	0
exp.	0.69	0.32	0.56	0.00	2.03	0.82	0.63	0.26	2.98
BB. FEORNT	1	2	13	0	13	0	0	2	0
exp.	2.22	1.02	1.88	0.00	6.57	2.64	2.05	0.85	9.64
CC. FEAPP	5	0	1	0	11	0	0	1	0
exp.	1.09	0.50	0.92	0.00	3.22	1.30	1.00	0.42	4.73
DD. SETTLE	0	1	0	0	10	5	0	1	1
exp.	1.37	0.63	1.16	0.00	4.06	1.63	1.27	0.53	5.96
EE. FELGFRNT	0	0	0	0	1	16	0	0	21
exp.	1.57	0.73	1.33	0.00	4.66	1.87	1.45	0.60	6.83
FF. TAP	0	0	0	0	1	5	0	0	4
exp.	0.44	0.20	0.36	0.00	1.31	0.53	0.41	0.17	1.93
GG. FEJMP	1	0	0	0	0	0	0	0	0
exp.	0.20	0.09	0.17	0.00	0.60	0.24	0.19	0.08	0.88
HH. FERUNA	1	3	0	0	9	0	24	0	0
exp.	1.06	0.95	1.74	0.00	6.09	2.45	1.90	0.79	8.93
Total:	26	12	22	0	77	31	24	10	113
Frequency:	0.04	0.02	0.03	0.00	0.12	0.05	0.04	0.02	0.18

Table 1.—Extended.

Following acts										
Tufted male		Female								
K. DISMINT	L. MLRU-NA	BB. FEOR-NT	CC. FEAPP	DD. SETTLE	EE. FELGF-RNT	FF. TAP	GG. FEJMP	HH. FERUNA	Row total	Row chi square
Tufted male										
0	0	8	0	0	0	0	0	0	8	73.95
0.76	0.36	0.69	0.35	0.41	0.50	0.17	0.06	0.79		
0	0	13	1	0	0	0	0	0	31	101.99
2.93	1.39	2.69	1.35	1.59	1.92	0.67	0.24	3.08		
0	0	6	1	0	0	0	0	1	12	34.41
1.13	0.54	1.04	0.52	0.61	0.74	0.26	0.09	1.19		
0	0	6	6	7	0	0	1	2	22	62.12
2.08	0.99	1.91	0.96	1.13	1.36	0.48	0.17	2.18		
0	0	0	0	0	0	0	0	0	0	
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
0	0	15	3	12	16	7	1	16	78	108.86
7.38	3.51	6.77	3.39	3.99	4.84	1.69	0.60	7.74		
0	0	0	0	1	10	0	0	2	32	68.55
3.03	1.44	2.78	1.39	1.64	1.98	0.69	0.25	3.18		
0	0	8	0	0	0	0	0	1	21	49.77
1.99	0.94	1.82	0.91	1.07	1.30	0.46	0.16	2.08		
0	0	0	0	0	1	0	0	2	10	9.17
0.95	0.45	0.87	0.43	0.51	0.62	0.22	0.08	0.99		
61	0	0	0	0	0	0	0	0	110	352.05
10.40	4.95	9.55	4.78	5.63	6.82	2.39	0.85	10.91		
0	12	0	0	0	1	0	0	24	66	93.16
6.24	2.97	5.73	2.87	3.38	4.09	1.43	0.51	6.55		
0	0	0	3	0	0	0	2	11	16	75.21
1.51	0.72	1.39	0.69	0.82	0.99	0.35	0.12	1.59		
Female										
0	0	0	0	0	0	0	0	0	17	372.6
1.61	0.76	1.48	0.74	0.87	1.05	0.37	0.13	1.69		
0	0	0	11	11	0	0	0	2	55	140.75
5.20	2.47	4.78	2.39	2.81	3.41	1.19	0.43	5.46		
0	2	0	0	2	3	0	0	2	27	36.26
2.55	1.21	2.34	1.17	1.38	1.67	0.59	0.21	2.68		
0	0	0	2	0	7	6	1	0	34	65.51
3.22	1.53	2.95	1.48	1.74	2.11	0.74	0.26	3.37		
0	0	0	0	0	0	1	0	0	39	143.29
3.69	1.75	3.39	1.69	2.00	2.42	0.85	0.30	3.87		
0	0	0	1	0	0	0	0	0	11	35.45
1.04	0.49	0.96	0.48	0.56	0.68	0.24	0.09	1.09		
0	1	0	0	0	2	0	0	1	5	18.57
0.47	0.22	0.43	0.22	0.26	0.31	0.11	0.04	0.50		
0	14	0	0	0	0	0	0	0	51	331.94
4.82	2.29	4.43	2.21	2.61	3.16	1.11	0.40	5.06		
61	29	56	28	33	40	14	5	64	645	2173.61
0.09	0.04	0.09	0.04	0.05	0.06	0.02	0.01	0.10		

are identical during another portion of the sequence.

Behavioral observations of courtship were conducted to elucidate the dramatic differences in male morphology and behavior of the two male morphs of *M. inclemens*. In order to quantify behavior differences between the morphs and evaluate female responses, the motor patterns unique to each morph, and female responses to those patterns, were analyzed using transition probability matrix methods.

METHODS

Immature and mature male and female *M. inclemens* were captured at several field sites in the local Cincinnati, Ohio (Hamilton County) area by hand and sweep net during the spring breeding season beginning in the early part of May (1988 through 1991). Spiders were maintained in the lab and housed in rectangular plastic containers, measuring 13 cm (l) × 7 cm (w) × 7 cm (h). A diet of domestic crickets (*Acheta domesticus*) and fruit flies (*Drosophila* sp.) was provided on a weekly basis, and water was available *ad libitum*.

Courtship behavior was observed in a rectangular arena constructed of plastic, measuring 18 cm (l) × 13 cm (w) × 4 cm (h). The inner sides were lightly coated with petroleum jelly to keep the spiders from climbing out. Females were placed into the arena first and after a short acclimation period, the male was introduced at the opposite end. Each female was randomly paired with an individual male (N = 91 females; with n = 48 tufted males; and n = 43 gray males) and tested once for response to male courtship. For transition matrix analysis, only those pairings that ended with copulation were used (n = 30 tufted; n = 24 gray).

Each courtship episode was videotaped using a JVC GX-N8 video camera and a JVC HRS-101 VHS format video cassette recorder. For each of the male-female pairings, a behavior sequence of preceding and following acts was recorded from videotape. In this manner, the communication of sexual receptivity behavior by the female to the male could be ascertained and differences between the males could be determined.

Male behaviors.—Following are the important male behaviors: MOVE (MLMVE): walking or swiveling before orienting to the female; ORIENT (MLORNT): swivel and alignment of the anterior median eyes toward a source of movement; APPROACH (MLAPP): directed walk toward the female, no leg or body posturing; STILT: stationary display in which the male stands up with the body off of the substratum. The abdomen is bent with the tip pointed toward the substratum, and the first pair of legs is held above the cephalothorax and waved vigorously lateral to medial and then medial to lateral. The palps are held with the tips toward the substratum and are waved in an up and down pattern. Intermittently, the male stands motionless with the legs outstretched and held above the cephalothorax (Fig. 1a; PRONE: male lowers the body to the substratum with the femurs held at 90° angles to the body and legs I & II pointed directly forward so that the tips overlap. After assuming this position, the male moves in a side to side semicircular motion (Fig. 1b); LEG CLAP (LGCLP): clapping legs I together 5–8 times/sec while zigzag dancing toward the female along her medial axis (Fig. 2); LEG FRONTAL (MLLGFRNT): first pair of legs are out-stretched and moved toward another spider, often touching the first pair of legs of the other individual; CHASE: running after a fleeing individual; JUMP (MLJMP): short leaps directed toward the other spider; MOUNT AND COPULATE (MNTCOP): male climbs over the cephalothorax of the female and lifts her abdomen to the side to allow insertion and sperm introduction; DISMOUNT (DISMNT): male uncouples with the female and backs off of her cephalothorax; MALE RUN AWAY (MLRNAW): turn and run quickly in the opposite direction of the other individual.

Female behaviors.—Following are important female behaviors: FEMALE MOVE (FEMVE): same as described for male; FEMALE ORIENT (FEORNT): same as described for male; FEMALE APPROACH (FEAPP): same as described for male; SETTLE: body is lowered to the substratum with legs I held to the front and directed toward the male; FEMALE LEG FRONTAL (FELGFRNT): same as described for the male; TAP: legs I are drummed rapidly on the substratum in a short burst; FEMALE JUMP (FEJMP): same as described for the male; FEMALE RUN AWAY (FERNAW): same as described for the male.

Transition matrix analysis.—Methods used to analyze preceding and following act behavior responses by male and female *M. inclemens* were adopted from Dingle (1969), Baylis (1976) and Nossek & Rovner (1984). Preceding and following behavioral events were organized into a transition probability matrix, in which each cell represents the total acts of behavior j following behavior i. The percent (P_{ij}) for each transition can be calculated by dividing total acts of behavior (j) by the corresponding row total. Expected values for each cell were calculated by multiplying the column frequency by corresponding row total (example from Table 1: column frequency for B. MLORNT = 0.04; row total for A. MLMVE = 8; expected for cell MLMVE/MLORNT = 0.04 × 8 × 0.32, etc.). Using the Yates' correction for estimating the individual χ^2 values for each cell in a row, the total row χ^2 value (with $df = 17$) could be generated (Tables 1 and 2). The sum of the row χ^2 values is equal to the χ^2 value for the entire matrix.

From the transition matrices, it was necessary to determine which of the dyads in a row were significant. To be conservative, only those rows with χ^2 values greater than 34 (i. e., significant at the 0.01 level) were considered in this analysis. Because it is incorrect to assign a statistical value to an individual cell with 0 *df*, a modified χ^2 value with 1 *df* was generated for each cell in an analyzed row. The equation for this cell χ^2 value is as follows:

Equation (1)

$$\frac{((|OB - EX|) - 0.5)^2}{EX} + \frac{(((|GT - OB|) - (|GT - EX|)) - 0.5)^2}{(GT - EX)}$$

Where: OB = Cell Observed Value; EX = Cell Expected Value; GT = Matrix Grand Total

RESULTS

There was a total of 91 female/male pairings; 48 with tufted males and 43 with gray males. Of these pairings, females copulated with 30 tufted males or 63% of the trials (in 37% of the trials copulation was not observed) and females copulated with 24 gray males or 55% of the trials (in 45% of the trials copulation was not observed). There was not a significant difference in copulation frequencies between male morphs (Yate's corrected $\chi^2 = 0.188$; $df = 1$; $P > 0.50$). Only those pairings that ended with copulation were used in the transition matrix analysis (n = 30 tufted morph; n = 24 gray morph).

For tufted male courtship behavior, the acts preceding were not independent of the acts following ($\chi^2 = 2173.61$; $df = 323$; $P < 0.001$; n = 30; Table 1). Similarly for gray male courtship behavior, the acts preceding were not independent of the acts following a behavior (χ^2 = 1695.01; $df = 323$; $P < 0.001$; $n = 24$; Table 2).

By estimating the χ^2 value for each cell of the matrix according to equation (1), significant dyads could be extracted. The following acts which significantly facilitate (i. e., greater than expected) and inhibit (i. e., less than expected) a preceding act at the 0.01 level with 1 degree of freedom were compared for each male morph (Table 3). The major difference in male response to female was the STILT behavior of the tufted male and the PRONE behavior of the gray male. While females oriented to the STILT display of the tufted morph more often, note that the effect of STILT and PRONE on female response was similar for both males (i. e., the female either approached the male or settled). There was a great deal of overlap in all other behaviors for males in response to the female. However, tufted males appear to facilitate more female behaviors with the leg clapping (LGCLP) behavior than the gray male and females were more likely to approach (FEAPP) or settle (SETTLE) after orienting to the tufted male. Importantly, the behaviors considered to be signals of female receptivity (i. e., approach and settle, leg frontal or tap) were produced by females similarly in response to both male types.

The matrices of male courtship behavior were then compared with each other to determine if males were responding differently to females and if there was a difference in female response to male courtship behavior. Matrices were compared by using the column totals in a chi square analysis. When STILT and PRONE were included in the analysis as separate behaviors, there was a significant difference between the two male matrixes ($\chi^2 = 58.45$; $df = 17$; $P < 0.01$). However, when STILT and PRONE were combined into one category, as Phase I, there was no significant difference between males ($\chi^2 = 13.88$; $df = 17$; $P > 0.50$).

An additional comparison of the two male courtship behavior matrices was made by comparing the observed values of one male morph using the transition probabilities of the other male type to generate expected values (see Baylis 1976). Transition probabilities for each preceding and

Table 2.—Gray morph transition matrix (*n* = 24 Gray males). Column of letters (far left) represents the corresponding behavior (e.g., A = MLMVE; BB = FEORNT, etc.). Top number in a row is the observed value and the bottom number is the expected value. Row Chi Square values are given in the far right column.

Preceding acts	Following acts: Gray male								
	B. MLOR-NT	C. MLAPP	D. STILT	E. PRONE	F. LGCLP	G. MLLG-FRN	H. CHASE	I. MLJMP	J. MNTCOP
Gray male									
A. MLMVE	0	0	0	0	0	0	0	0	0
exp.	0.13	0.07	0.00	0.14	0.25	0.10	0.12	0.10	0.61
B. MLORNT	0	5	0	4	2	0	0	0	0
exp.	0.86	0.45	0.00	0.95	1.68	0.68	0.82	0.64	4.05
C. MLAPP	0	0	0	2	0	0	0	1	0
exp.	0.43	0.23	0.00	0.48	0.84	0.34	0.41	0.32	2.02
D. STILT	0	0	0	0	0	0	0	0	0
exp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
E. PRONE	0	0	0	0	2	0	0	0	0
exp.	0.95	0.50	0.00	1.05	1.85	0.75	0.90	0.70	4.45
F. LGCLP	0	0	0	0	0	2	0	7	0
exp.	1.68	0.89	0.00	1.86	3.28	1.33	1.60	1.24	7.89
G. MLLGFRN	0	0	0	0	0	0	0	0	12
exp.	0.65	0.34	0.00	0.72	1.26	0.51	0.61	0.48	3.03
H. CHASE	0	0	0	1	5	0	0	0	0
exp.	0.56	0.30	0.00	0.62	1.09	0.44	0.53	0.41	2.63
I. MLJMP	0	0	0	0	0	0	0	0	9
exp.	0.56	0.30	0.00	0.62	1.09	0.44	0.53	0.41	2.63
J. MNTCOP	0	0	0	0	0	0	0	0	38
exp.	3.84	2.02	0.00	4.25	7.48	3.03	3.64	2.83	18.00
K. DISMNT	0	0	0	2	11	0	0	0	12
exp.	2.33	1.23	0.00	2.58	4.54	1.84	2.21	1.72	10.92
L. MLRUNA	0	0	0	0	0	0	0	0	0
exp.	0.56	0.30	0.00	0.62	1.09	0.44	0.53	0.41	2.63
Female									
AA. FEMVE	17	0	0	0	0	0	0	0	0
exp.	0.73	0.39	0.00	0.81	1.43	0.58	0.70	0.54	3.44
BB. FEORNT	1	5	0	10	9	0	1	1	0
exp.	1.38	0.73	0.00	1.53	2.69	1.09	1.31	1.02	6.47
CC. FEAPP	1	0	0	2	0	1	0	1	0
exp.	0.65	0.34	0.00	0.72	1.26	0.51	0.61	0.48	3.03
DD. SETTLE	0	0	0	0	1	2	0	0	2
exp.	0.78	0.41	0.00	0.86	1.51	0.61	0.74	0.57	3.64
EE. FELGFRNT	0	0	0	0	1	7	0	2	16
exp.	1.17	0.61	0.00	1.29	2.27	0.92	1.10	0.86	5.46
FF. TAP	0	0	0	0	2	3	0	1	0
exp.	0.39	0.20	0.00	0.43	0.76	0.31	0.37	0.29	1.82
GG. FEJMP	0	0	0	0	2	0	0	0	0
exp.	0.13	0.07	0.00	0.14	0.25	0.10	0.12	0.10	0.61
HH. FERUNA	0	0	0	0	2	0	17	1	0
exp.	1.21	0.64	0.00	1.34	2.35	0.95	1.15	0.89	5.66
Total:	19	10	0	21	37	15	18	14	89
Frequency:	0.04	0.02	0.00	0.05	0.08	0.03	0.04	0.03	0.20

Table 2.—Extended.

Following acts										
Gray male		Female								
K. DISMNT	L. MLRU-NA	BB. FEOR-NT	CC. FEAPP	DD. SETTLE	EE. FELGF-RNT	FF. TAP	GG. FEJMP	HH. FER-UNA	Row total	Row chi square
Gray male										
0	0	3	0	0	0	0	0	0	3	53.12
0.35	0.14	0.20	0.11	0.12	0.18	0.08	0.02	0.28		
0	0	9	0	0	0	0	0	0	20	87.83
2.32	0.95	1.36	0.73	0.77	1.23	0.50	0.14	1.86		
0	0	4	1	1	0	0	1	0	10	19.33
1.16	0.48	0.68	0.36	0.39	0.61	0.25	0.07	0.93		
0	0	0	0	0	0	0	0	0	0	
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
0	0	1	8	6	0	2	0	3	22	90.97
2.55	1.05	1.50	0.80	0.85	1.35	0.55	0.15	2.05		
0	0	3	2	6	12	1	0	6	39	85.55
4.52	1.86	2.66	1.42	1.51	2.39	0.98	0.27	3.63		
0	0	0	0	0	3	0	0	0	15	30.38
1.74	0.72	1.02	0.55	0.58	0.92	0.38	0.10	1.40		
0	0	7	0	0	0	0	0	0	13	51.32
1.51	0.62	0.89	0.47	0.50	0.80	0.33	0.09	1.21		
0	0	1	0	1	0	0	0	2	13	16.68
1.51	0.62	0.89	0.47	0.50	0.80	0.33	0.09	1.21		
51	0	0	0	0	0	0	0	0	89	224.7
10.32	4.25	6.07	3.24	3.44	5.46	2.23	0.61	8.29		
0	12	0	0	0	1	0	0	16	54	77.48
6.26	2.58	3.68	1.96	2.09	3.31	1.35	0.37	5.03		
0	0	2	0	0	0	0	0	11	13	76.71
1.51	0.62	0.89	0.47	0.50	0.80	0.33	0.09	1.21		
Female										
0	0	0	0	0	0	0	0	0	17	345.9
1.97	0.81	1.16	0.62	0.66	1.04	0.43	0.12	1.58		
0	0	0	3	0	0	0	0	2	32	88.21
3.71	1.53	2.18	1.16	1.24	1.96	0.80	0.22	2.98		
0	0	0	0	2	4	3	1	0	15	27.64
1.74	0.72	1.02	0.55	0.58	0.92	0.38	0.10	1.40		
0	0	0	2	0	4	5	1	1	18	47.75
2.09	0.86	1.23	0.65	0.70	1.10	0.45	0.12	1.68		
0	0	0	0	1	0	0	0	0	27	61.34
3.13	1.29	1.84	0.98	1.04	1.66	0.68	0.18	2.52		
0	0	0	0	0	3	0	0	0	9	28.99
1.04	0.43	0.61	0.33	0.35	0.55	0.23	0.06	0.84		
0	1	0	0	0	0	0	0	0	3	33.72
0.35	0.14	0.20	0.11	0.12	0.18	0.08	0.02	0.28		
0	8	0	0	0	0	0	0	0	28	247.39
3.25	1.34	1.91	1.02	1.08	1.72	0.70	0.19	2.61		
51	21	30	16	17	27	11	3	41	440	1695.01
0.12	0.05	0.07	0.04	0.04	0.06	0.03	0.01	0.09		

Table 3.—A comparison of preceding behaviors that significantly facilitate (observed value greater than expected) or inhibit (observe value less than expected) the following behaviors. Column of letters (far left) represents the corresponding behavior (e.g., A = MLMVE; BB = FEORNT, etc.). Chi square analysis: $df = 1$ for each dyad; $P < 0.01$.

Behavior	Tufted		Gray	
	Facilitates	Inhibits	Facilitates	Inhibits
Male				
A. MLMVE	BB		BB	
B. MLORNT	C, D, BB		C, E, BB	
C. MLAPP	D, BB		BB	
D. STILT	BB, CC, DD		********	
E. PRONE	********		CC, DD	
F. LGCLP	BB, DD, EE, FF, HH	F, J	I, DD, EE	J
G. MLLGFRN	J, EE		J	
H. CHASE	F, BB		F, BB	
I. MLJMP	********		********	
J. MNTCOP	J, K	F, BB, HH	J, K	F, HH
K. DISMNT	L, HH		F, L, HH	
L. MLRUNA	GG, HH		HH	
Female				
AA. FEMVE	B		B	
BB. FEORNT	D, CC, DD	J	C, E, F	
CC. FEAPP	B, F		EE, FF	
DD. SETTLE	F, EE, FF		EE, FF	
EE. FELGFRNT	G, J		G, J	
FF. TAP	G		G, EE	
GG. FEJMP	********		********	
HH. FERUNA	H, L	J	H, L	

following act were calculated by dividing the observed frequency for each cell in a row by its corresponding row total (example calculated from Table 1 cell A. MLMVE / BB. FEORNT the transition probability = 8/8 = 1.00 etc.). By this analysis, using the observed values of the tufted male, and the transition probabilities of the gray male to generate the expected, there was no significant difference between observed and expected values ($\chi^2 = 151.23$; $df = 323$; $P > 0.5$) for the matrix. The behaviors that resulted in significantly greater and fewer acts for the tufted male compared to the gray male are shown in Table 4a. When tufted males performed the leg clapping behavior, females oriented and displayed a greater number of tap displays to them than to the gray morph. Furthermore, females responded to tufted morph leg clapping with more settle displays than to the gray male. Additionally, after a female oriented, the tufted male responded with fewer PRONE displays than the gray male. Likewise, using the observed values of the gray male compared to the expected values generated by the transition probabilities of the tufted male, there was no significant difference between the males ($\chi^2 = 74.61$; $df = 17$; $P > 0.5$). The acts that were greater and fewer for the gray male over the tufted male are shown in Table 6. After the female oriented, gray males approached the female more often than the tufted male. Additionally, the gray male responded to the female with fewer STILT displays than the tufted male.

As a final analysis and comparison of the courtship behavior of the two male morphs, frequency diagrams were constructed showing the transition probability from one behavior to the next (Fig. 3). For these diagrams, behaviors were sorted into discrete categories where [a] Phase I represents the initial phase of courtship (i. e., the males are some distance from the female) and the diagnostic behaviors were STILT for the tufted male and PRONE for the gray male, [b] Phase II represents male distance reducing behaviors (i. e., male approaches the female) and the diagnostic behavior was the LEG CLAP display, [c] Receptivity behaviors were discrete signals by the female to the male that were followed by Phase II or Copulatory behaviors, [d] Copulatory behaviors involved male and female coupling, and [e] Postcopulatory behaviors were those that occurred after the male and female coupled.

Comparing the two diagrams, the frequency diagram of tufted male (Fig. 3a) shows more complexity in behaviors related to Phase II courtship than that of the gray male. However, the overall trend in the behavior sequences was similar for the two different male morphs.

Table 4.—A comparison of preceding-following event pairs with: (a) Tufted morph as observed and using the observed frequencies of the Gray morph to calculate expected values; and (b) Gray morph as observed and using the observed frequencies of the Tufted morph to calculate expected values. Column of letters (far left) represents the corresponding behavior (e.g., A = MLMVE; BB = FEORNT, etc.). Chi square analysis: $df = 1$ for each dyad; $P < 0.01$. * Chi square = 151.23; $df = 323$; $P > 0.1$. † Chi square = 74.61; $df = 323$; $P > 0.1$.

	(a) Tufted as observed*		(b) Gray as observed†	
Behavior	Greater	Fewer	Greater	Fewer
Male				
A. MLMVE				
B. MLORNT				
C. MLAPP				
D. STILT				
E. PRONE				
F. LGCLP	BB, FF			
G. MLLGFRN				
H. CHASE				
I. MLJMP				
J. MNTCOP				
K. DISMNT				
L. MLRUNA				
Female				
AA. FEMVE				
BB. FEORNT		E	C	D
CC. FEAPP				
DD. SETTLE	F			
EE. FELGFRNT				
FF. TAP				
GG. FEJMP				
HH. FERUNA				

DISCUSSION

The behavior patterns exhibited by *M. inclemens* were, in general, similar to those described for other jumping spider species (Crane 1949; Cutler 1988; Forster 1982; Jackson 1977a, 1977b, 1981a, 1981b, 1982). The courtship sequence of most jumping spiders can be subdivided into three stages or phases (see Forster 1982). In Phase I, the males attract the attention of the female and species identification takes place. After species identification, females indicate acceptance (often by simply remaining motionless) and males approach the female (Phase II). Finally, in Phase III, males mount the female and they copulate, after which the male dismounts and the two individuals uncouple. The behaviors reported in the frequency diagrams (Fig. 3) fit this general model for salticid courtship behavior.

Unlike many salticid species where females indicate receptivity by remaining stationary (Crane 1949; Forster 1982), female *M. inclemens* respond to male courtship behavior with a visual receptivity display that may take several forms or indicate relative willingness to mate. Females may indicate receptivity by simply approaching the male. However, the approach is typically followed by settling, and tapping legs I rapidly on the substratum or leg frontals toward the male. Often there is body posturing and repositioning where the female tips her abdomen from side to side. All of these behaviors may be performed during the courtship sequence, although generally only one of the above responses is sufficient as a signal for the male to mount and copulate. Indeed, females that gave the tap display to the courting male were observed to mate 100% of the time.

While the overall sequence of courtship behavior does not appear to differ between the two male morphs, including behaviors unique to each morph (i. e., STILT and PRONE) does result in statistically significant differences between male morphs. In the initial phase of courtship (Phase I), the STILT display was used exclusively by tufted males and the PRONE display was used exclusively by gray males. Each of these unique Phase I behaviors was diagnostic of the morph and genetically linked to the morphology of the male (Clark 1992). Ultimately, the information conveyed to the female by the STILT and PRONE displays was similar; both displays cause females to either approach the male or settle. Consequently, each display, while unique, appears to transmit species specific (and morph specific) information to the female. After receiving a sexual

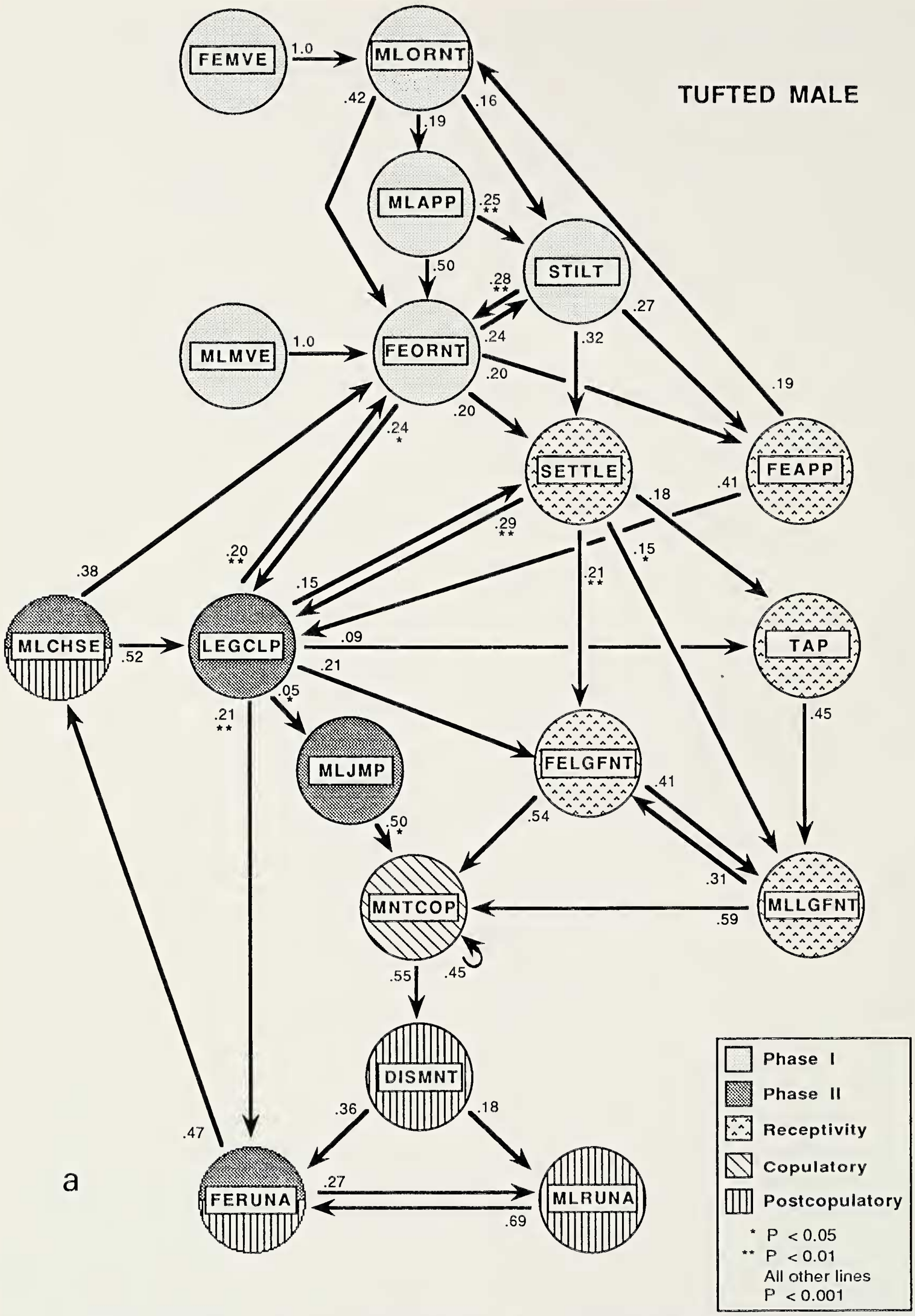

Figure 3a.—Sequence diagrams of male courtship behavior of the tufted morph of *Maevia inclemens*. Numbers indicate the percent each transition from one behavior to the next occurred.

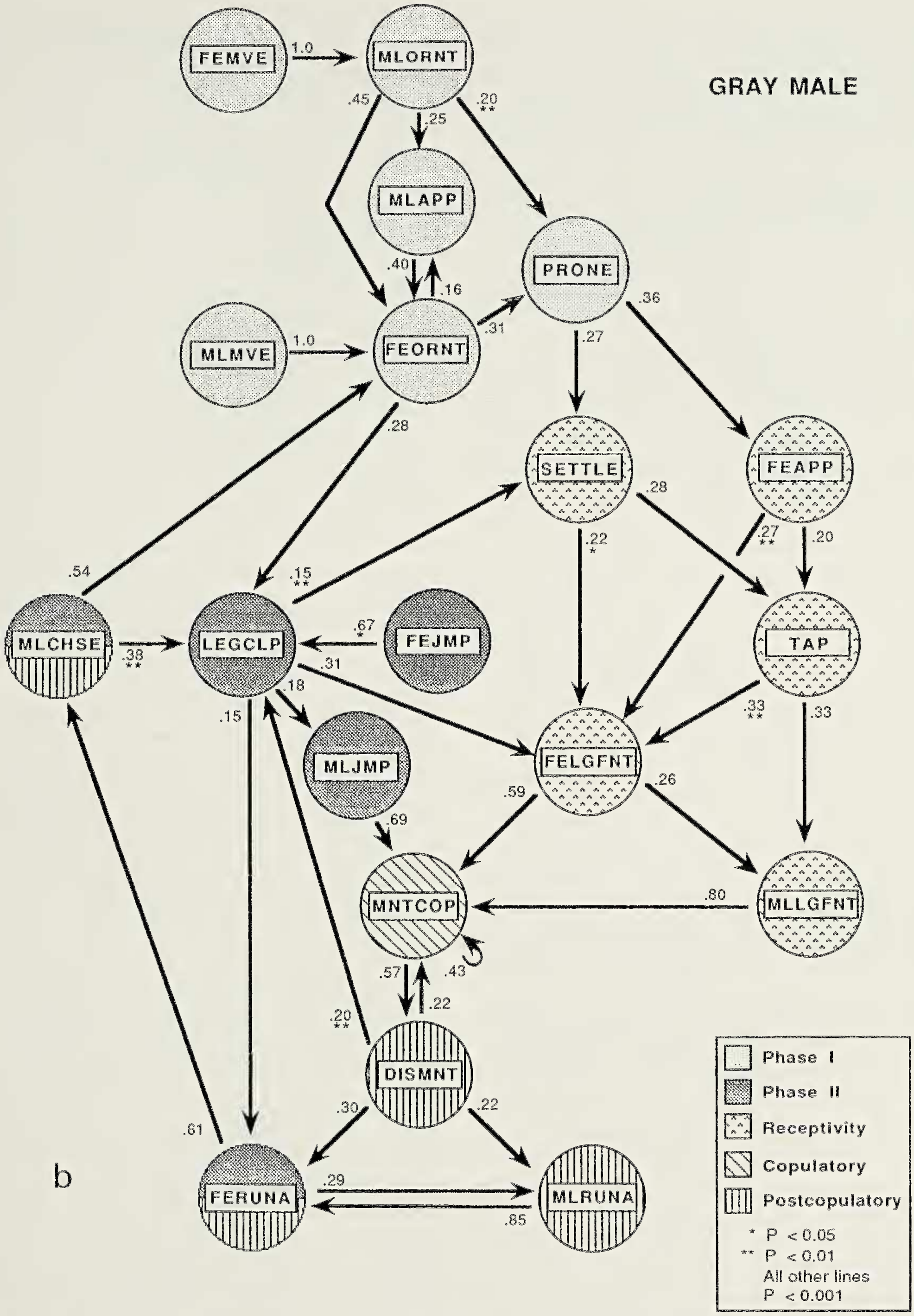

Figure 3b.—Sequence diagrams of male courtship behavior of the gray morph of *Maevia inclemens*. Numbers indicate the percent each transition from one behavior to the next occurred.

receptivity display from the female, each morph typically ceases Phase I display and starts leg clapping and zig-zag dancing (Phase II). This Phase II behavior typically leads to leg frontal displays by the female and is typically followed by leg frontals by the male. Finally the male mounts and copulates with the female, after which the male dismounts and the two individuals typically run away from each other (Phase III). Variations on this theme do occur, and the male may sometimes chase the female and attempt to copulate with her again.

From the observations reported here it seems that Peckham & Peckham (1889) were incorrect in their description of the gray morph courtship behavior. However, it is also possible that the specimens observed by Peckham & Peckham represent some geographical variant of this species. Results from this study support Painter's (1913) observation that gray morphs do not assume an upright posture in the context of courtship. While it is difficult to know the context of the gray morph display that the Peckhams described, it is possible that they mistakenly described a male threat display (Clark 1992) instead of a courtship display. Additionally, earlier descriptions by Peckham & Peckham (1889) and Painter (1913) did not comment on the presence of leg clapping behavior by tufted males. Results presented here indicate that tufted males were as likely to perform leg clapping behavior in the same context as the gray males. Indeed, both males typically performed this behavior after Phase I and when approaching the female. Furthermore, males rarely reverse the order of Phase I and Phase II motor patterns.

Little is known about the evolution of male dimorphism within this species. Peckham & Peckham (1889) suggested that the gray morph was the primitive or ancestral form and that the tufted morph was the more recently evolved morph. W. Maddison (pers. comm.) also contends that the gray morph is likely to be the ancestral form based on a species comparison of the genus *Maevia* and the developmental patterns of *M. inclemens* (all juveniles resemble the gray morph until the penultimate molt; Clark 1992). The Peckhams (1889) hypothesized that the tufted morph evolved by sexual selection through female mate choice. However, Painter (1913) conducted experiments to determine the extent of female preference and found that females do not show a preference for the tufted males. Additionally, using videotaped sequences of male courtship behavior, Clark & Uetz (1992) determined that female mate choice depends on the male that moves first, and this was independent of male morphology.

While females may not show a mate preference for one male morph over the other, it is likely that the two male morphs have evolved as alternative reproductive strategies, where the function of the Phase I courtship display is different for each morph. Analysis of frequency diagrams showed that tufted males used the STILT display to capture the attention of females (as demonstrated by females orienting to a stilting tufted male). This may serve to attract female attention from greater distances as Clark & Uetz (1993) recently demonstrated that tufted males initiate courtship an average of 86 mm from the female (compared to the gray male which initiates courtship an average of only 34 mm from the female). The courtship distance of the tufted male may also account for greater complexity in the male to female interactions related to distance reducing behaviors (Phase II), as shown in the frequency diagrams.

While courtship distance and complexity may represent a potential cost to tufted males (i. e., approaching the female may require more energy or females may be lost from view more frequently), it was demonstrated that the mating success of both male morphs was approximately equal. This suggests that the costs related to the courtship distance of the tufted morph may be offset by some, as yet, unknown selective benefit. As demonstrated by Clark & Uetz (1992), attracting female attention first had a significant positive effect on male mating success. It is hypothesized that tufted males may simply be more conspicuous to females at greater distances (by using the STILT display) and they exploit a predisposed female response to movement. Furthermore, the STILT display of tufted males may facilitate contrast against cryptic or moving backgrounds. This hypothesis is supported experimentally by Fleishman (1988), who demonstrated for anoline lizards that displays which are initially rapid and out of phase with background movement are the most efficient at attracting attention from another individual. The rapid leg movements of the tufted male coupled with contrasting black and white coloration may serve a similar purpose. In contrast, the gray male does not use the PRONE display to capture female attention, rather it is more likely to approach the female after she has oriented and then it assumes this posture. The striking colors of the palps may function as a signal that differentiates the gray male from a potential prey item at close distances to the female. Future studies will be conducted to investigate these hypotheses.

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